A NEGLECTED MONOGRAPH ON FOLIAR HISTOGENESIS

ADRIANCE S. FOSTER

Within recent years, an awakened interest in developmental problems, especially in connection with the theory of periclinal chimaeras, has led to a number of studies on leaf differentiation in angiosperms (5). Unfortunately, however, little or no effort has been made towards comparative investigations within a genus or family, so that most of these contributions are distinctly isolated in character. Investigators in this field have returned in vain for guidance and orientation to the classical works of anatomists of the past century, but here the emphasis was largely upon the early phases of leaf initiation, rather than upon the later stages of development. Consequently, the writer feels justified in calling attention to an unique monograph on the comparative histogenesis of leaves which has remained unnoticed by anatomists since its publication in 1872.[1] This article is from the pen of Samsøe Lund (7) and bears the title "The calyx of the Compositae: essay on the unity of development in the vegetable kingdom." The original Danish text is accompanied by a complete French translation. The extensive scope of this remarkable memoir does not permit of concise summation, but an effort will be made to indicate certain facts and conclusions which deserve consideration in the light of modern studies on leaf ontogeny.

The writer wishes to thank Dr. G. L. Stebbins, Jr., for calling his attention to Lund's monograph.

Lund maintains that, ideally, we should describe the differentiation of a leaf in terms of the formation of all its cells. However, since the practical difficulties of this goal are so great in most cases, Lund devotes the first part of his treatise to the histogenesis of a presumably simple "foliar" structure, viz., the pappus of the composite flower. In some species, for example, *Cirsium arvense,* the pappus is differentiated into an epidermal, fundamental, and vascular system. In other instances, internal tissue (which he terms "endophyll") is greatly reduced in amount or absent and the histogenesis of the pappus resembles a trichome. However, both of these extremes appear to be connected by intergrading forms and Lund concludes that the pappus is foliar in nature and, hence, a true calyx. Although Lund's morphological interpretation of the pappus may not be completely acceptable in its original form, it seems to the writer that further histogenetic studies of this structure, along comparative lines, would be extremely profitable.[2]

---

[1] Among the few references on this work, known to the writer, are a brief and wholly inadequate review by McNab (9) and a cursory note by Small (13).

[2] In a later paper Lund (8) defended his viewpoint against the objections of

MADROÑO, Vol. 3, pp. 321–384, October 28, 1936.

With the relatively simple histogenesis of the pappus as a guide, Lund next presents the results of a wide series of observations on the apical, marginal, and intercalary formation of cells in various types of foliar organs. It is significant to note, first of all, that he rejects Hanstein's (6) concept of dermatogen, periblem, and plerome, at least in respect to the apical and marginal meristems of the leaf. Lund maintains, on the contrary, that such meristems are composed at most of two regions, viz.: (a) the *pycnome,* which is formed apically or laterally as a "solid" tissue, and (b) the *périnome,* which arises apically or laterally as one or more discrete layers of cells. Thus, the pycnome is equivalent to Hanstein's plerome, while the périnome includes *both* the dermatogen and the periblem layers. Lund's viewpoint becomes decidedly modern in spirit when it is realized that more than fifty years later, Schmidt (12) adopted a similar viewpoint towards the structure of the angiospermous growing point. He classified primordial meristem into the *tunica* (= périnome) and the *corpus* (= pycnome), a distinction which has been profitably adopted by many recent investigators (cf. Foster [5], p. 352, footnote 3). In an effort to demonstrate the "unity of development," which underlies the morphogenesis of the leaves of all vascular plants, Lund states that considerable plasticity exists in the relationship and behavior of the pycnome and périnome regions of a leaf meristem. In some cases, a périnome may be absent (at least during the latter stages in development) and then marginal or apical growth resembles that of a leptosporangiate fern (cf. Bower [2]). Furthermore, the périnome, in a given organ, may change its method of cell formation and become a pycnome. Thus, Lund argues, the distinction between trichomes and phyllomes, as well as between leaf development in cryptogams and phanerogams, rests upon a quantitative, rather than a qualitative, basis. Lund defends this thesis most ably by his description of the behavior of the marginal meristem in various leaf types at successive stages in their development. His observations in this point are so pertinent to certain recent studies that a brief résumé may be of value.

The marginal meristem, which he terms the "growing line," consists, in the simplest case, of a single series of marginal initials (t_1 in figs. 43[3], 44) which by periclinal or alternating oblique divisions produce, respectively, a uniseriate or biseriate wing of tissue. This condition obtains during the final stages in growth of the involucral bracts of many composites and the bud scales of *Taxus*. More commonly, however, the marginal meristem consists of one or more layers of périnome investing a central pycnome.

Warming (14, p. 23–27) and presented additional observations on the apical growth of the pappus in *Senecio vulgaris*.

[3] Figures referred to are those of Lund's illustration, reproduced as text figure 1.

In this case, each layer of the périnome is formed by a series of marginal initials which divide by anticlinal non-convergent walls (t_1, figs. 45, 46; t_1–t_2, figs. 47, 48). The pycnome, however, is generated by a line of initials which divide either periclinally (t_2, fig. 45; t_3, fig. 47) or obliquely (t_2, fig. 46; t_3, fig. 48), thus simulating the behavior of the simple type of marginal meristem illustrated by figures 43–44.

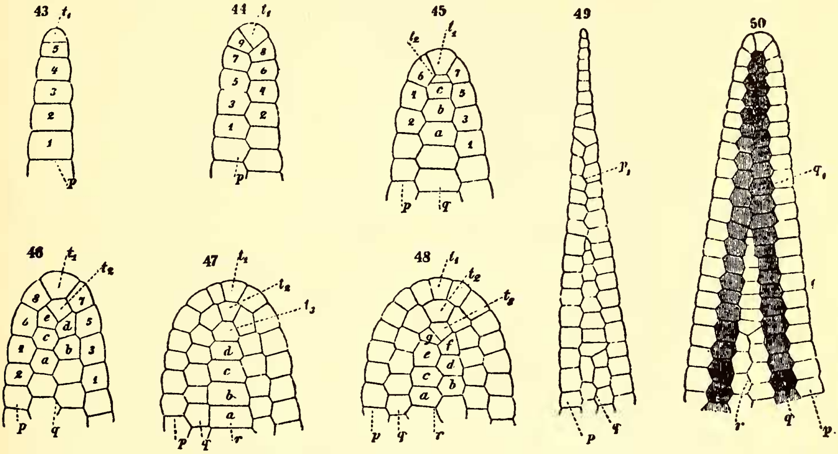

Fig. 1. Diagrams illustrating various types of marginal meristem in the foliar organs of angiosperms. The numbers or letters indicate the sequence of cell lineages. Abbreviations: *p*, outer layer of périnome; *q*, inner layer of périnome; *r*, pycnome. Further explanation in text. (From Lund.)

The distribution of these latter types of marginal meristem is interesting. The condition illustrated in figure 48 occurs in the majority of angiospermous genera investigated by Lund and the following examples may be quoted as illustrations: *Cirsium, Vinca, Cynoglossum, Viola, Vitis, Lamium, Helianthemum.* Figure 47 illustrates another frequent type which Lund observed in various species of *Rumex* and *Polygonum* and in many members of the Chenopodiaceae. A distinctive type of marginal growth is represented by figure 46, which illustrates the situation in many species of *Begonia,* as well as in some genera of the Gesneriaceae and Piperaceae. Lund carefully emphasizes the interesting fact that while some of these types of marginal growth are consistent throughout the whole course of ontogeny (e.g., figs. 47, 48), in other types the structure of the marginal meristem changes from a "high" to a "low" degree, in respect to the behavior of the initial cells as marginal growth diminishes. For example, in *Begonia,* Lund found that the pycnome at first is produced by alternating oblique divisions of the initials (fig. 46), while later these same initials divide periclinally, as is illustrated in figure 45. A more striking illustration is furnished by the bud scale of *Taxus.* Here, at first, the pycnome originates as in the *Begonia* type (fig. 46), but later develops as is shown in figure 45. Finally, all further cell formation at the edge of the pycnome ceases and the perinome itself merges into a biseriate and ultimately uniseriate plate of cells. This complex process is clearly illustrated in figure 49. A similar transition from one type of marginal growth to another is illustrated by the development of the involucral bracts of some composites (fig. 50).

In conclusion, it may be pointed out that certain recent investigations confirm the value of Lund's provisional survey of marginal growth in the leaf. In *Carya Buckleyi* var. *arkansana* (4) and in *Heterotrichum* and *Clidemia* (15) the marginal meristem behaves similarly to the *Begonia* type as described by Lund (cf. fig. 46). The recent investigations of Cross (3) clearly show that marginal growth in the bud scales of *Morus alba* L. is identical with the situation in the cataphylls of *Taxus* as described by Lund. Although this type of marginal differentiation may prove upon further study to be characteristic of many bud scales, bracts, and sepals, it also obtains in the foliage leaves of certain monocotyledons, according to the recent studies of Pottier (11; pls. 16, 18, 35). In *Pelargonium* (10) and *Nicotiana* (1) the situation most closely resembles the type described by Lund as common to many angiosperms (cf. fig. 48), except that the "submarginal initials" are described as dividing *both* anticlinally and periclinally. Possibly, the marginal growth in *Pelargonium* and *Nicotiana* represents a condition intermediate in character between two of Lund's types. In any event, the problem of marginal growth in foliar organs demands further comparative study. It seems to the writer, however, that in all future investigations of foliar differentiation, the data and interpretations of Lund should prove a helpful source of orienation, and that his memoir should be accorded its rightful position among the anatomical classics of the nineteenth century.

University of California, Berkeley,
April 21, 1936.

Literature Cited

1. Avery, G. S., Jr. Structure and development of the tobacco leaf. Amer. Jour. Bot. 20: 565–592. 1933.
2. Bower, F. O. The comparative examination of the meristems of ferns, as a phylogenetic study. Ann. Bot. 3: 305–392. 1889.
3. Cross, G. L. The structure of the growing point and the development of the bud scales of Morus alba L. Bull. Torr. Bot. Club. 1936. (In press.)
4. Foster, A. S. A histogenetic study of foliar determination in Carya Buckleyi var. arkansana. Amer. Jour. Bot. 22: 88–147. 1935.
5. ————. Leaf differentiation in angiosperms. Bot. Rev. 2: 349–372. 1936.
6. Hanstein, J. Die Scheitelzellgruppe im Vegetationspunkt der Phanerogamen. Festschr. der Niederrhein Ges. Natur.-u. Heilkunde: 109–143. 1868.

7. LUND, SAMSØE. Baegeret hos Kurvblomsterne, et histologisk forsøg på at haevde udviklingens enhed i planteriget. Bot. Tidsskrift Anden Raekke 2: 1–120, figs. 1–50. 1872. (Translated into French as "Le calice des Composées. Essai sur l'unité du developpement dans le règne végétal." Ibid.: 121–260.)
8. ————. Bemaerkninger om Baegeret hos Kurrblomsterne. En Antikritik. Videnskabelige Meddelelser naturhist. Forening Kjöbenhavn 5: 75–122, taf. III (30 fig.). 1873. (Résumé in French under title "Observations sur le calice des Composées"; une anticritique. Ibid.: pp. 10–37.)
9. McNAB, W. R. Review of Samsøe Lund's monograph. Jour. Bot. n. s. 2: 184. 1873.
10. NOACK, K. L. Entwicklungsmechanische Studien an panaschierten Pelargonien. Jahrb. Wiss. Bot. 61: 459–534. 1922.
11. POTTIER, J. Contribution a l'étude du devéloppement de la racine de la tige et de la feuille des phanerogames angiospermes. Les monocotylédones marines méditérranéenes Ruppia maritima L., Cymodocea nodosa (Ucria) Anderson et Posidonia oceanica (L.) Delile de la famille des Potamogétonacées. Besancon. Jacques et Demontrand. pp. 125. 52 pl. 1934.
12. SCHMIDT, A. Histologische Studien an phanerogamen Vegetationspunkten. Bot. Archiv. 8: 345–404. 1924.
13. SMALL, J. The origin and development of the Compositae. New Phyt. 17: 75. 1918.
14. WARMING, E. Om Forskjellen mellem Trichomer oq Epiblastemer af höjere Rang. Vidensk. Medd. Natur. For. Kjöbenhavn 4 (10–12): 159–205, pls. I–IX, 1872. (Résumé in French under title "Sur la difference entre les trichomes et les èpiblastèmes d'unordre plus élevé." Ibid.: pp. 16–27.)
15. WEIDT, E. Die Entwicklung der Blätter der Melastomataceen Heterotrichum macrodon Planch. und Clidemia hirta Don. Beitr. z. Biol. d. Pflan. 23: 252–281. 1935.

A NATURAL VIOLET HYBRID

VIOLA BRAINERD BAIRD

Viola Douglasii × purpurea hyb. nov. Planta aspectu *V. Douglasii* similis, herbae retrorso-pubescens vel canescens. Folia ambitu oblonga vel rhombico-ovata, in segmentis apiculatis, attenuatis irregulariter pinnate incisa vel divisa; stipulae foliorum basalium eis *V. Douglasii* similes, sed angustiores. Petala ut ea *V. purpurea* tincta. Pistillum ut in *V. purpureo* ovario glabro excepto. (Plate XVIII, fig. 2).

Type. Collected in Walker Basin, between Bodfish and Caliente, Kern County, Sequoia National Forest, California, altitude about 6000 feet, April 18, 1935, *Viola Brainerd Baird* (University of California Herbarium no. 545986).

The hybrid was growing with the two parent species on an open sunny hillside which was covered with *Plagiobothrys nothofulvus.* It was more vigorous than either parent. There were three plants in one cluster, one of which bore eighteen flowers and numerous buds. Further search failed to yield more material, indicating that the two species do not hybridize freely. The respective points of resemblance of the hybrid to the parent species are shown in Table I.